

**Barley Yellow Dwarf Virus Isolate-Specific Resistance in Spring
Oats Reduced Virus Accumulation and Aphid Transmission**

by

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2 Virus Accumulation and Aphid Transmission

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15 Abstract

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17 specific resistance in spring oats reduced virus accumulation and aphid
18 transmission. *Phytopathology*

19 Resistance to barley yellow dwarf virus in a spring oat genotype was
20 manifested as a reduction in accumulation of viral antigen in whole plants. The
21 resistance was quantified for five isolates of BYDV from New York (MAV,
22 PAV, SGV, RPV and RMV) and found to be BYDV isolate-specific. Similar
23 levels of resistance were quantified for MAV, PAV, and SGV in which the
24 reduction in viral antigen ranged from 58-63%, relative to levels in a susceptible
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1 genotype. RMV antigen was reduced up to 82%, but no resistance was
2 expressed against the RPV isolate. Reduced viral antigen was correlated with
3 reduced levels of transmission of MAV, PAV, SGV and RMV, but not RPV.
4 Further reductions in transmission efficiency were possible by limiting the
5 acquisition access period. Resistance to circulative, nonpropagative, aphid-borne
6 viruses manifested as a reduction in virus antigen may reduce the spread of
7 disease among plants, especially if coupled with aphid resistance manifested as
8 a feeding deterrent.
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11 Barley yellow dwarf virus (BYDV) is responsible for serious economic loss
12 in all major cereal crops worldwide. Despite intensive efforts during recent
13 decades to identify high levels of resistance (3) only limited success has been
14 achieved. In recent years varying levels of resistance to BYDV manifested as a
15 reduction in viral antigen or viral RNA accumulation have been reported for
16 wheat, barley and oat (2, 10, 11, 19, 22). The mechanisms of resistance are only
17 beginning to be understood (10) and the resistance may be expressed at different
18 levels within the same genotype depending on the isolate of BYDV infecting the
19 plant (2, 9, 19). It was suggested that a reduced virus concentration may
20 translate to reduced aphid transmission efficiency and reduced virus spread (8,
21 21). This correlation is well documented for nonpersistent viruses (5), but has
22 received only limited attention for persistent viruses (1). Virus concentration
23 can affect acquisition efficiency for some virus isolate-aphid vector combinations,
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1 but additional factors, such as length of feeding time or virus distribution in
2 plants, may have more of an effect on overall transmission efficiency (1, 6).

3 We describe a resistance in a spring oat genotype that is manifested as a
4 reduction in the accumulation of viral antigen. The resistance was examined in
5 relation to its effectiveness against five BYDV isolates from New York. In
6 addition, we examined the influence reduced viral antigen had on aphid
7 transmission efficiency.

8 MATERIALS AND METHODS

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10 Virus isolates, aphid vectors and host genotypes. The BYDV isolates used
11 in these studies included the previously characterized NY-BYDV isolates
12 referred to as PAV, MAV, RPV, RMV and SGV (15, 17). All isolates were
13 maintained in 'Coast Black' oats (*Avena byzantina* K. Koch) as described by
14 Rochow (15).

15 The aphids used in all experiments were clonally propagated from aphids
16 originally collected and described by Rochow using his methods and rearing
17 conditions (15). In all the studies PAV and RPV were transmitted by
18 *Rhopalosiphum padi*, MAV by *Sitobion avenae*, RMV by *R. maidis*, and SGV by
19 *Schizaphis graminum*.

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21 Plant genotypes included a winter oat cultivar, Coast Black, which is
22 susceptible to all the NY isolates of BYDV, and a spring oat cultivar, Ogle,
23 found to possess field resistance to PAV in New York (4). In addition, a
24 breeding accession, IL86-5262, developed at the University of Illinois and kindly
25 provided by Dr. Charles Brown was included. IL86-5262 was field tested at

1 Cornell University in 1987 and 1988 and found to possess high levels of field
2 resistance to PAV (Gray, unpublished).

3 **Virus antigen accumulation studies.** Virus antigen measured by ELISA and
4 expressed as absorbance values (A_{405}), was quantified in plants one to six weeks
5 following inoculation. Ten day old seedlings of Coast Black, Ogle and IL86-5262
6 were inoculated with the various isolates of BYDV by the appropriate aphid
7 vector. Viruliferous aphids (10/plant) were given a 96 h inoculation access
8 period on the seedlings in a growth chamber maintained at 21 C. Aphids were
9 killed by fumigation with DDVP (O,O-dimethyl-O-[2,2-dichlorovinyl]phosphate)
10 in a closed chamber, and test plants were placed in a greenhouse. Six plants of
11 each genotype were inoculated each week for 6 wk. Subjective evaluation of
12 each plant for BYDV symptom expression was performed weekly by comparing
13 infected plants to non-inoculated plants grown under similar conditions. Leaf
14 discoloration and overall plant height were evaluated. At the end of the 6 wk
15 period all plants were harvested by removing the aerial portions of the plants
16 (i.e. 36 plants of each genotype; 6 plants from each wk, 1-6 wk post-inoculation).
17 Sap was extracted from leaves and small stems of individual plants using a
18 rolling leaf press. A 250 μ l aliquot of sap from each sample was diluted 1:5 with
19 PBS (phosphate buffered saline) and 200 μ l loaded into duplicate wells of a
20 microtiter plate previously coated with immunoglobulin (2 μ g/ml, 2 h at 37C)
21 prepared against homologous purified virions. Double antibody sandwich ELISA
22 (DAS-ELISA) was conducted as previously described (6). The production and
23 specificity of the antisera to the NY-PAV, NY-MAV and NY-RPV isolates have
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been described elsewhere (16). Antisera to the NY-RMV and NY-SGV isolates were produced in Dr. Richard Lister's laboratory (21). In our hands the antisera to NY-RMV or NY-SGV only react with the homologous antigen in DAS-ELISA. To allow direct comparisons of absorbance values of unknown samples among plates, a 2-fold dilution series of purified virus diluted in healthy sap and representing the linear portion of a standard curve was included on each plate. The absorbance values of the 6 standards plus a healthy sap control were monitored during the substrate reaction and the entire plate was read when the standards reached a similar predetermined pattern of absorbance values ranging from $A_{405} = 1.5$ to $A_{405} = 0.05$ for the highest and lowest dilution, respectively. Absorbance values of unknown samples fell within the range of the standards a majority of the time.

Absorbance data (= viral antigen titer) were analyzed with analysis of variance following a log transformation of the data. All analyses were done with the ANOVA or ONEWAY programs of Minitab (12). The relationship between weekly viral antigen titer and genotype was examined for each virus isolate individually using a completely random design. Genotype, week and the genotype by week interaction were all tested against the error sum of squares. Analysis of variance was also used to compare 6 wk mean viral antigen titers between genotypes and pairwise differences were calculated using Tukey's test with an error rate of $\alpha = 0.05$ (13).

Virus transmission studies. Five seedlings of Coast Black and IL86-5262 were inoculated with each of the five BYDV isolates as above and allowed to

grow in the greenhouse for 3 wk. Twenty aphids (4th instars for *R. padi* and *S. avenae*, 1st-2nd instars for *R. maidis* and *S. graminum*) were caged on the youngest fully expanded leaf (4th or 5th) of the main tiller of each plant and allowed a 24 h acquisition access period (AAP). Single aphids were then transferred to individual, healthy oat seedlings (Coast Black) and allowed a 48-72 h inoculation access period. Aphids were killed by fumigation with DDVP in a closed chamber, and test plants were placed in a greenhouse and observed for symptom expression for 4-5 wk. Transmission efficiency was calculated as the proportion of 20 aphids transmitting virus from each source leaf. A mean transmission efficiency was calculated from the five source leaves. The entire experiment was conducted five times; therefore, transmission efficiency for each isolate/aphid combination was calculated using 500 aphids (20 x 5 x 5).

To determine the effect of the length of AAP on the transmission efficiency of BYDV from the resistant and susceptible genotypes experiments similar to those described above were performed with the following changes. The transmission of RMV by *R. maidis* was tested using a 2 h and a 6 h AAP; and transmission of MAV by *S. avenae* was tested using a 6 h AAP; and transmission of RPV by *R. padi* was tested using a 2 h AAP. Individual experiments to determine the transmission efficiency from five individual source leaves of each genotype (20 aphids/source) were conducted four times.

To estimate the amount of virus antigen in each source leaf used in all the transmission experiments, the section of leaf enclosed by the cage was excised

1 immediately following transfer of the aphids to indicator plants and virus antigen
2 content was immediately quantified by DAS ELISA as described above.

3 Two types of data were analyzed with analysis of variance: the percentage
4 of aphids that successfully transmitted the virus from each plant genotype; and
5 the viral antigen titer in source leaves. All analyses were done with the GLM
6 program of Minitab (12). A log transformation was used to transform the viral
7 antigen titer data prior to analysis and the arcsin-square root transformation was
8 used to transform the binomial transmission data prior to analysis.
9 Untransformed data are presented in Tables and Figures. The relationship
10 between plant genotype and transmission, and between plant genotype and viral
11 antigen titer was examined for each virus isolate individually using a randomized
12 complete block design. Each transmission experiment using five source leaves
13 was treated as a replication. Accordingly genotype was tested against the
14 genotype by experiment sums of squares. The model was run both with and
15 without absorbance values as a covariate to determine whether the effect of
16 cultivar on transmission depended on viral antigen titer. The experiments using
17 different AAP's were analyzed independently and no attempt was made to
18 include AAP as a variable in the ANOVA.
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21 RESULTS

22 **Virus Symptom Expression.** Symptom severity and type were BYDV isolate
23 dependent in all genotypes (Table 1). Coast Black plants all exhibited classical
24 BYDV reddening and stunting regardless of which BYDV isolate was infecting
25 the plant. The severity of the symptoms was variable depending on the BYDV

isolate; PAV, MAV and RPV caused more severe symptoms than RMV or SGV. Symptom expression in Ogle was less severe than in Coast Black. PAV, MAV and RPV all caused yellow-red leaf discoloration, but symptoms tended to ameliorate as the plants matured. Slight stunting was evident in all plants. Except for an occasional yellow leaf, all Ogle plants infected with RMV or SGV were symptomless. All IL86-5262 plants remained symptomless regardless of the infecting BYDV isolate, with the exception of one plant infected with PAV exhibited slight yellowing 2-3 wk post inoculation.

Virus antigen accumulation. The pattern of virus antigen accumulation in plants over the 6 wk was variable within and among cultivars and BYDV isolates (Fig. 1). Analyses to determine differences in viral antigen titer utilized all data points, but compared mean antigen levels over the 6 wk period. Ogle and IL86-5262 both possess resistance to 4 of 5 BYDV isolates that is manifested as a reduction in the amount of viral antigen accumulating in leaf tissue; however the level of resistance varies between plant genotype and among BYDV isolates. The reduction in relative levels of antigen accumulating in resistant vs susceptible genotypes over the 6 wk experiment were similar for PAV, MAV and SGV. Relative to levels in susceptible Coast Black plants (set at 100%), mean levels of MAV antigen were reduced to 64% and 39% in Ogle and IL86-5262, respectively; PAV antigen was reduced to 57% and 35%, in Ogle and IL86-5262, respectively; and SGV antigen was reduced to 50% and 42% in Ogle and IL86-5262, respectively (Fig. 1). There was no significant difference ($P = 0.744$) in mean levels of RPV antigen accumulating in leaf tissue of the three genotypes.

Levels of RMV antigen were reduced to 22% and 20% in Ogle and IL86-5262, respectively, relative to levels in Coast Black (100%).

Pairwise comparisons of mean viral antigen titer between genotypes indicated antigen levels were significantly lower ($P = 0.05$) in both Ogle and IL86-5262 plants than in the susceptible Coast Black plants for MAV, PAV, SGV and RMV. Differences in viral antigen titer between Ogle and IL86-5262 were significant ($P = 0.05$) only for MAV and PAV (Figure 1).

Our experience indicates that IL86-5262 was more difficult to inoculate with RMV by *R. maidis* than Ogle or Coast Black. The percentage of IL86-5262 plants inoculated with RMV by *R. maidis* and having an ELISA value above healthy background was 27% compared to 55% and 88% infection of Ogle and Coast Black, respectively. The percent infection of all genotypes with the other BYDV isolate-vector combinations was 100%. Inoculation of the three genotypes with RMV using *R. maidis* was repeated using 15-20 viruliferous aphids per plant. Infection levels were 96%, 96% and 88% for Coast Black, Ogle and IL86-5262, respectively. Plants from the second experiment were used to determine the accumulation of RMV antigen in the three genotypes.

Virus transmission. Virus source tissue was chosen by leaf position and time after inoculation to maximize differences in viral antigen (based on ELISA) between resistant IL86-5262 and susceptible Coast Black tissue. Generally the youngest fully expanded leaf was used on plants three weeks post-inoculation. In all experiments there was significantly less viral antigen ($P = 0.05$) in source tissue from IL86-5262 than Coast Black plants (Table 2). Mean viral antigen

titer was reduced by 67%, 82%, 66% 45% and 89% for PAV, MAV, SGV, RPV and RMV, respectively in the resistant IL86-5262 relative to susceptible Coast Black tissue. The differences between mean viral antigen titers in IL86-5262 and Coast Black plants were consistent in all five replicates of experiments using the five virus isolates (data not shown).

Mean transmission efficiency was consistently lower from the resistant IL86-5262 tissue relative to Coast Black for each of the virus isolate-aphid vector combinations (Table 2). Transmission efficiency of RPV by *R. padi* was significantly lower from IL86-5262 than Coast Black with ($P = 0.002$) or without ($P = 0.028$) viral antigen as a covariate indicating viral antigen titer in the source tissue was not responsible for the difference in transmission efficiency. Transmission efficiencies of MAV by *S. avenae* and RMV by *R. maidis* were significantly lower from the IL86-5262 tissue when transmission data were analyzed independent of viral antigen titer (MAV, $P = 0.048$; RMV $P = 0.004$). When viral antigen titer was used as a covariate in the analysis differences in transmission efficiency from IL86-5262 and Coast Black virus sources were not significantly different (MAV, $P = 0.322$; RMV $P = 0.187$) indicating that viral antigen titer did contribute significantly to the differences in transmission efficiency. Differences in transmission efficiency of PAV by *R. padi* or SGV by *S. graminum* from IL86-5262 or Coast Black were not significant (PAV, $P = 0.177$) or barely significant (SGV, $P = 0.07$) when transmission data were analyzed independent of viral antigen titer. If viral antigen titer was used in the analysis the levels of significance were, $P = 0.997$ and $P = 0.485$ for PAV and

1 SGV, respectively. This relatively large decrease in levels of significance for
2 PAV and SGV transmission efficiencies when viral antigen titer was used in the
3 analyses suggests that in addition to other unknown factors, the reduction in
4 virus titer may have had a significant effect on the ability of aphids to acquire
5 virus from IL86-5262 plants.

6 Reducing the length of AAP reduced the transmission efficiency of the
7 three BYDV isolate-aphid vector combinations examined (Table 3). The
8 transmission efficiency of RMV by *R. maidis* was 6.8% and 20.0% when given
9 a 6 hr AAP and 0% and 2.5% when given a 2 h AAP from IL86-5262 and Coast
10 Black, respectively. Due to the low mean transmission rate and large numbers
11 of aphids not transmitting virus no further analysis was done on data resulting
12 from the 2 h AAP experiment. In contrast to the transmission study on RMV
13 using a 24 h AAP the difference in transmission efficiency of RMV from either
14 source using a 6 h AAP was not significantly different, although transmission
15 efficiency was influenced by viral antigen titer. The transmission efficiencies of
16 MAV by *S. Avenae* were 38.6% and 50% when given a 6 hr AAP on IL86-5262
17 and Coast Black, respectively (Table 3). Differences in transmission efficiencies
18 between the two sources were not significantly different (MAV $P = 0.084$) and
19 viral antigen titer did not significantly influence transmission efficiency. The
20 transmission efficiency of RPV by *R. padi*, given a 2 hr AAP, was 20.5% and
21 23.2% from IL86-5262 and Coast Black, respectively. The difference was not
22 significant ($P = 0.250$) and viral antigen did not significantly influence
23 transmission efficiency.

The viral antigen titer differences between IL86-5262 and Coast Black for the MAV RPV and RMV were significant and similar to those described previously (Table 3).

DISCUSSION

Resistance or tolerance to BYDV in small grains is generally assessed based on symptoms induced by one isolate (4, 7, 10, 11, 22). Rarely are multiple isolates used to assess resistance (2, 9, 19, 22). Studies of this nature have shown a correlation between degree of resistance (measured by yield parameters or virus titer) and symptom severity (7, 10), although exceptions do exist (19). Our findings generally agree with previous studies that a susceptible variety, e.g. Coast Black, will show symptoms when infected with any of the NY BYDV isolates whereas genotypes with various levels of resistance to BYDV, e.g. Ogle or IL86-5262, will show reduced or no symptoms. However, our work has shown that symptom appearance and/or severity may not reflect the level of resistance to virus accumulation in the plant and that virus resistance is BYDV isolate-specific. None of the NY BYDV isolates produced consistent symptoms in IL86-5262 yet clearly resistance levels, with regard to viral antigen titer, range from very high in the case of RMV to completely susceptible in the case of RPV. Symptom expression in Ogle is also not reflective of viral antigen titer. RPV infection induces milder symptoms than PAV or MAV yet the resistance to virus accumulation in whole plants was not detected for RPV.

Transmission efficiency from the resistant IL86-5262 plants was reduced for all five NY BYDV isolates, but viral antigen titer did not contribute significantly

1 to the reduction in transmission of RPV. Gray *et al.* (6) also found that
2 transmission of NY-RPV by *R. padi* was not influenced by viral antigen titer. A
3 commonality of both studies was the inability to examine virus sources that
4 varied widely with respect to viral antigen titer. It is likely that the transmission
5 efficiency of RPV by *R. padi* can be influenced by virus concentrations, but that
6 the virus concentrations necessary to show this have not been used.

7 The reduction in viral antigen titer in IL86-5262 did contribute to the
8 significant reduction in transmission efficiency of MAV, PAV, SGV and RMV;
9 however, the magnitude of the difference in viral antigen titer between IL86-
10 5262 and Coast Black tissue was not reflective of the difference in transmission
11 efficiency. In general, transmission efficiency was high for all aphid-virus
12 combinations regardless of virus source or viral antigen titer. The most striking
13 example was the ability of 38% of *R. maidis* individuals to transmit RMV from
14 IL86-5262 tissues that had a mean viral antigen titer not significantly above
15 healthy background as determined by ELISA.

16 It was not determined if fewer aphids were acquiring the MAV, PAV, SGV
17 and RMV from the IL86-5262 tissue and reducing the probability of transmission
18 or if all aphids were acquiring less virus which reduces their ability to transmit.
19 The later explanation is more probable based on the findings of Barker and
20 Harrison (1) and van den Heuval *et al.* (20) in which aphids were found to
21 acquire less virus when fed either on plants with a lower virus titer or an
22 artificial diet containing less virus. The acquisition of less virus by most aphids
23 rather than fewer aphids acquiring virus is somewhat supported by the fact that
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1 reducing the AAP reduces the transmission efficiency of aphids regardless of the
2 source (Table 3). If the reduction in transmission was due to fewer aphids
3 acquiring virus there should be fewer aphids transmitting from the resistant
4 source relative to the susceptible source regardless of the AAP. Reducing the
5 AAP appears to have reduced the amount of virus acquired from either source
6 to levels below a threshold necessary for transmission. The reduction in viral
7 antigen titer effectively increases the time necessary for aphids to acquire enough
8 virus for transmission. This hypothesis is supported by the finding of Gray *et al.*
9 (6) who showed that the effect of virus titer was only important at short AAP
10 and given enough time an aphid could acquire enough virus to become
11 viruliferous regardless of the titer.

12 It is important that programs screening for BYDV resistance recognize the
13 limitations of using symptom severity as a sole selection criteria and the
14 probability that resistance to one BYDV isolate may not indicate resistance to
15 all isolates of BYDV. Screening should be done against all BYDV isolates
16 common to the particular geographic region and selection should be made not
17 only on yield considerations, but also on increasing resistance to the virus to
18 minimize the potential for the crop to serve as a symptomless reservoir for
19 BYDV. The results of this study suggest that virus antigen concentration may
20 be useful screening technique to identify and distinguish virus resistance from
21 tolerance. As previously discussed, reduced viral antigen titer correlates with
22 reduced symptoms and increased yield in many instances. Additionally, this
23 study and others (6, 19) indicate that a reduction in viral antigen titer can

1 significantly reduce the transmission efficiency of certain luteovirus isolates by
 2 their respective aphid vectors. Since the effect of titer on transmission efficiency
 3 is dependent on the length of AAP it would be of benefit to combine this type
 4 of resistance with one that limits the length of time an aphid will feed on a plant
 5 (14).
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Table 1. Relative virus symptom expression^a in three oat genotypes caused by five New York isolates of barley yellow dwarf viruses.

Virus isolate	Oat genotype	Symptom type ^b
PAV	Coast Black	Y S
	Ogle	y S
	IL86-5262	NS ^c
MAV	Coast Black	Y S
	Ogle	y S
	IL86-5262	NS
SGV	Coast Black	y S
	Ogle	s
	IL86-5262	NS
RPV	Coast Black	Y S
	Ogle	y s ^d
	IL86-5262	NS
RMV	Coast Black	y s
	Ogle	s
	IL86-5262	NS

^aRelative symptom intensity was assessed, on plants grown in a greenhouse, weekly from 1-6 wks following inoculation.

^bY Yellowing and/or reddening of most leaves on all plants

y Yellowing and/or reddening may occur on the first 1-3 leaves developing on an indicator plant 2-3 wk post inoculation. Symptoms never observed in new growth of plants >3 wk post inoculation.

S Severe stunting

s Slight stunting

NS No symptoms

2 of 36 plants showed yellowing of 1-2 leaves

^dYellow/red leaf discoloration was prominent on first 1-2 leaves, but new growth was asymptomatic.

Table 2. Comparison of barley yellow dwarf viral antigen titer (measured by ELISA) in leaf tissue of two oat genotypes and the transmission efficiency of aphid vectors acquiring virus from the two source tissues.

Virus isolate ^a	Oat genotype ^b	Viral antigen titer ^c (A_{405})	Transmission efficiency ^d
PAV	Coast Black	0.672 ± 0.104	84 ± 4.8
	IL86-5262	0.223 ± 0.042	76 ± 6.4
		$P = 0.010$	$P = 0.177 (0.997)$
MAV	Coast Black	0.544 ± 0.033	81 ± 2.6
	IL86-5262	0.099 ± 0.012	68 ± 2.9
		$P = 0.001$	$P = 0.048 (0.332)$
SGV	Coast Black	0.530 ± 0.138	59 ± 9.3
	IL86-5262	0.183 ± 0.031	46 ± 12.1
		$P = 0.012$	$P = 0.070 (0.485)$
RPV	Coast Black	0.378 ± 0.049	63 ± 8.0
	IL86-5262	0.206 ± 0.033	52 ± 7.8
		$P = 0.005$	$P = 0.002 (0.028)$
RMV	Coast Black	0.350 ± 0.083	69 ± 6.8
	IL-5262	0.040 ± 0.006	38 ± 4.8
		$P < 0.001$	$P = 0.004 (0.187)$

^aBarley yellow dwarf isolates from New York and transmitted by their efficient aphid vector; RPV - *Rhopalosiphum padi*, RMV - *R. maidis*, PAV - *R. padi*, MAV - *Sitobion avenae*, SGV - *Schizaphis graminum*.

^bPlants were inoculated 3-4 wk prior to use as a source, the youngest fully expanded leaf was used (4th or 5th leaf). Coast Black plants are considered to be susceptible to all 5 NY BYDV isolates. IL86-5262 plants possess varying levels of resistance to the 5 NY BYDV isolates expressed as a reduction in viral antigen titer.

^cValues are the mean \pm standard error of mean absorbance data (A_{405} nm) read directly from ELISA plates (2 wells/sample). Five plants were used for each experiment and each experiment was replicated 5 times ($n = 25$). P value indicates the significance level of the difference between the two values.

^dAphids were allowed a 24 h acquisition access period before being transferred to Coast Black oat seedlings (one aphid per seedling) for a 5-7 day inoculation access period. The transmission efficiency represents the mean percentage \pm standard error ($n = 500$) of infected indicator plants for five experiments repeated over time and using five source plants (leaves) for each experiment. Twenty indicator plants were used to determine the transmission efficiency from each source leaf. P values indicate the significance level of the difference between the transmission efficiencies from Coast Black oats and oat breeding line IL86-5262. The P values in parentheses were calculated with viral antigen titer data as a covariate in the analysis.

Table 3. Effect of acquisition access period on aphid transmission efficiency of selected BYDV isolates from two oat genotypes.

Virus isolate/ aphid vector ^a	Oat genotype	Length of AAP ^b	Virus antigen titer ^c (A_{405})	Transmission efficiency ^d
MAV/ <i>S. avenae</i>	IL86-5262	6 hr	0.150 ± 0.087	$38.6\% \pm 5.9$
	Coast Black		0.713 ± 0.087	$50\% \pm 6.1$
			$P = 0.013$	$P = 0.084 (0.121)$
RPV/ <i>R. padi</i>	IL86-5262	2 hr	0.248 ± 0.041	$20.5\% \pm 5.5$
	Coast Black		0.478 ± 0.060	$23.2\% \pm 6.1$
			$P = 0.012$	$P = 0.250 (0.293)$
RMV/ <i>R. maidis</i>	IL86-5262	6 hr	0.049 ± 0.026	$6.8\% \pm 4.7$
	Coast Black		0.428 ± 0.107	$20.0\% \pm 6.5$
			$P = 0.007$	$P = 0.126 (0.653)$

^aBYDV isolates and aphid clones characterized and maintained from New York.

^bAcquisition Access Period.

^cValues are the mean \pm standard error of mean absorbance data (A_{405} nm) read directly from ELISA plates (2 wells/sample). Five plants were used for each experiment and each experiment was replicated 4 times ($n = 20$). P value indicates the significance level of the difference between the two values.

^dFollowing the acquisition access period aphids were transferred to BYDV-susceptible Coast Black indicator seedlings (one aphid per seedling) for a 5-7 day inoculation access period. The transmission efficiency represents the mean

percentage \pm standard error ($n = 400$) of infected indicator plants for four experiments repeated over time and using five source plants (leaves) for each experiment. Twenty indicator plants were used to determine the transmission efficiency from each source leaf. *P* values indicate the significance level of the difference between the transmission efficiencies from Coast Black oats and oat breeding line IL86-5262. The *P* values in parentheses were calculated with viral antigen titer data as a covariate in the analysis.

Figure 1. The temporal pattern of accumulation of barley yellow dwarf virus antigen, as determined by ELISA, in a susceptible oat genotype, Coast Black, and two oat genotypes possessing isolate-specific resistance to BYDV, Ogle and IL86-5262. Mean levels of antigen ($n = 3-6$) accumulating in the aerial portions of plants 1-6 wk post-inoculation are indicated for 5 New York BYDV isolates. Bars from left to right (in each 6 bar group) represent wk 1-6, respectively. Percentages given below each 6 bar group indicate the 6 wk mean level of virus antigen relative to 6 wk mean antigen levels in the susceptible Coast Black genotype. Percentages followed by the same letter are not significantly different ($P = 0.05$) in pairwise comparisons of 6 wk mean levels of antigen.

Virus Antigen (ELISA) in Plants 1 --> 6 Weeks After Inoculation

